CORRELATION OF ALKALINITY AND THE DISTRIBUTION OF *POTAMOGETON* IN NEW ENGLAND[1]

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The abundance of lakes and streams in New England provides for a wide variety of aquatic plants. The two main drainage areas in the region are the coastal watershed, with the major rivers draining to the Atlantic Ocean, and the St. Lawrence River watershed. The chemical quality of these waters varies due to the general substrate of a specific area, farming runoff, and pollution. Much of the region lacks any calcareous substrate, hence the waters are often acidic or neutral. The acidic areas occur mainly in the sandy regions of the coastal drainage and the granitic regions inland. This includes all of Rhode Island, most of New Hampshire and Massachusetts, and parts of Maine, Vermont, and Connecticut. Alkaline areas occur over the limestone regions of northeastern Maine, most of Vermont, extreme western Massachusetts and parts of western and southern Connecticut.

The many floristic publications (Fernald, 1950; Gleason, 1952; Fassett, 1957) and some monographs on the genus *Potamogeton* (e.g. Hagström, 1916; Fernald, 1932; Ogden, 1943) indicate that some species of *Potamogeton* occur mainly in acid, alkaline, or brackish waters. A survey of the literature revealed only two studies on the distribution of aquatic macrophytes and water chemistry in the United States. These were carried out by Steenis (1932) in Wisconsin and by Moyle (1945) in Minnesota. Spence (1967) noted plants commonly found in waters of different alkalinities from Scotland.

This investigation was conducted in an attempt to define the ranges of the species of *Potamogeton* in New England in relation to the chemical properties of the waters in which they grow. Initially, pH, total alkalinity, free carbon dioxide, nitrates, total phosphates and chlorides were tested (Hellquist, 1975). Total alkalinity presented the highest correlation with the other factors tested and *Potamogeton* distribution, hence will be discussed here.

The nomenclature in this paper follows Fernald (1950), with modifications of some taxa by Haynes (1974) and Reznicek and Bobette

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(1976). These authors recognize 40 taxa in northeastern United States and southeastern Canada, while in New England 37 varieties of 30 species are identified.

SAMPLING AND STATISTICAL PROCEDURES

Field work was conducted at 321 locations throughout New England (Figure 1). Total alkalinity tests followed the procedure of Theroux et al. (1943). Total alkalinity was expressed as mg $CaCO_3$ per liter and converted to mg HCO_3^- per liter to correspond with results indicated in Hutchinson (1975). Many of the sites and regions were chosen beforehand by consulting the herbaria of the University of New Hampshire, Harvard University, and the New England Botanical Club. In these herbaria, specimens noted by many authors (e.g. Fernald, 1932; Ogden, 1943) as alkaline ("hard") or acidic ("soft") water plants were utilized to determine water-quality regions of New England. This procedure was of particular value for locating rarer plants of such regions.

Means, medians, and ranges of the alkalinity were calculated for each species found in at least five field locations. Separations or cluster formation was sought by placing all data into a distribution of difference between means on the basis of alkalinity. A one-way design analysis was conducted to test for significant differences among the six resulting clusters on means other than that on which they had been segregated. A second analysis showed that real difference among the means were present after the clusters were made (Hellquist, 1975).

RESULTS AND DISCUSSION

The means, medians, and ranges of the alkalinities for all taxa are found in Table 1. *Potamogeton filiformis* var. *macounii, P. vaginatus, P. hillii, P. lateralis, P. diversifolius,* and one hybrid *P.* × *longiligulatus,* were not found at a sufficient number of locations to make computation of the summary data meaningful. Figure 3 indicates the alkalinity range of *Potamogeton* taxa found in New England waters.

Statistical means for the major watersheds studied in New England (Figure 2) reveal that the alkaline regions occur in western New England and the St. John River drainage of Aroostook County, Maine. A comparison of these values with plant distribution discloses a marked effect of alkalinity in the range of *Potamogeton* in New England.

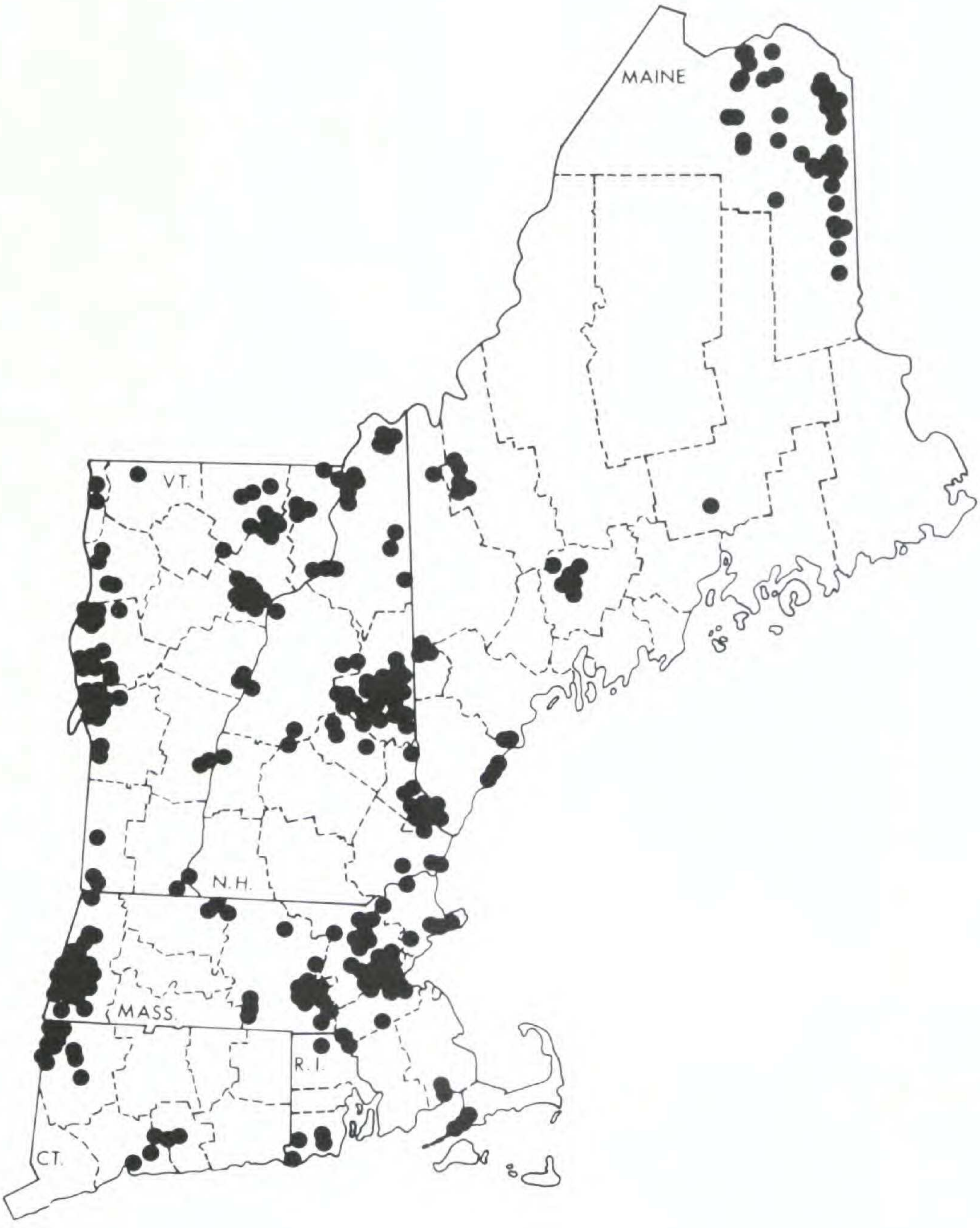

Figure 1. Sampling locations in New England.

Table 1.

Occurrence of New England *Potamogeton* and observed alkalinity in lake and stream waters.*

Species	Alkalinity (mg HCO_3^- liter^{-1}) Mean	Median	Range	Number Analyses
P. filiformis Pers. var. *borealis* (Raf.) St. John	80.5	77.5	29.3–107.4	10
P. filiformis Pers. var. *macounii* Morong	92.8	103.7	67.1–107.4	3
P. vaginatus Turcz.	125.7	125.7		1
P. pectinatus L.	114.5	112.9	36.6–282.5	26
P. robbinsii Oakes	28.8	25.6	3.7–122.0	49
P. crispus L.	84.9	93.4	14.6–207.5	31
P. confervoides Reichenb.	4.2	4.3	0.6– 8.5	12
P. zosteriformis Fern.	60.2	48.8	5.5–150.7	74
P. foliosus Raf.	77.1	73.2	17.1–167.8	62
P. friesii Rupr.	86.9	84.8	42.7–150.7	11
P. strictifolius Ar. Benn.	84.8	87.3	67.1–109.8	5
P. pusillus L. var. *pusillus*	74.5	68.3	30.5–139.7	21
P. pusillus L. var. *gemmiparus* Robbins	10.5	11.0	3.1– 15.9	8
P. pusillus L. var. *tenuissimus* Mert. & Koch	36.9	19.5	3.1–206.3	143
P. × *longiligulatus* Fern.	103.3	109.8	87.3–112.9	3
P. hillii Morong	148.6	135.5	135.5–161.7	2
P. obtusifolius Mert. & Koch	58.3	58.5	16.5–127.5	18

Table 1 (continued)

P. lateralis Morong	16.5	16.5		1
P. vaseyi Robbins	26.6	25.6	8.5– 54.9	11
P. spirillus Tuckerm.	19.2	13.4	3.1– 70.2	78
P. diversifolius Raf.	2.4	2.4		1
P. bicupulatus Fern.	7.6	5.5	1.8– 25.6	32
P. epihydrus Raf. var. *epihydrus*	65.6	70.2	11.0–122.0	15
P. epihydrus Raf. var. *ramosus* (Peck) House	21.6	13.4	2.4–161.7	154
P. alpinus Balbis var. *tenuifolius* (Raf.) Ogden	41.0	23.8	4.9–140.3	24
P. alpinus Balbis var. *subellipticus* (Fern.) Ogden	60.8	59.8	12.2–127.5	18
P. amplifolius Tuckerm.	35.6	28.1	4.3–150.7	78
P. pulcher Tuckerm.	11.7	10.4	3.7– 46.4	21
P. nodosus Poir.	88.8	75.7	6.1–282.5	20
P. gramineus L. var. *gramineus*	39.0	25.0	3.1–150.7	85
P. gramineus L. var. *maximus* Morong	18.9	15.3	3.7– 67.1	15
P. gramineus L. var. *myriophyllus* Robbins	22.9	20.1	4.3– 95.2	17
P. illinoensis Morong	82.9	79.9	24.4–150.7	24
P. natans L.	41.4	20.7	3.1–161.7	152
P. oakesianus Robbins	8.8	6.1	2.4– 24.4	33
P. praelongus Wulfen	56.4	43.9	9.8–150.7	39
P. richardsonii (Ar. Benn.) Rydb.	53.2	43.9	16.5–130.6	27
P. perfoliatus L. var. *bupleuroides* (Fern.) Farw.	36.3	23.8	6.1–167.8	46
total of sampling locations	43.0	24.2	0.6–282.5	321

**Taxa with less than five observations are not included in the statistical analysis*

1	Androscoggin River	6.47 HCO_3^- (mg liter^{-1})
2	Saco River	6.59
3	Thames River	8.13
4	Rhode Island – southeastern Massachusetts	9.64
5	Kennebec and Penobscot Rivers	10.92
6	Merrimac River	11.69
7	New Hampshire seacoast	20.54
8	eastern Massachusetts	27.11
9	Connecticut River	37.28
10	coastal ponds and streams	40.44
11	St. John River	56.38
12	Hudson River	74.11
13	St. Lawrence River	81.04
14	Housatonic River	95.33

Figure 2. Mean alkalinities of major New England watersheds from present study.

The clusters (Table 2) determined in this study provide a basis for the classification of New England waters. Many *Potamogeton* species may occur over a wide range of alkalinities (Figure 3) encom-

Table 2

Classification of New England waters determined by clusters of *Potamogeton* taxa most commonly found in them.

Group	Taxa
Group I—alkalinity 0.0–18.3 mg HCO_3^- liter^{-1}	*P. confervoides*
	P. bicupulatus
	P. oakesianus
	P. pusillus var. *gemmiparus*
	P. pulcher
Group II—alkalinity 18.4–30.5 mg HCO_3^- liter^{-1}	*P. gramineus* var. *maximus*
	P. spirillus
	P. epihydrus var. *ramosus*
	P. gramineus var. *myriophyllus*
	P. vaseyi
	P. robbinsii
Group III—alkalinity 30.6–48.8 mg HCO_3^- liter^{-1}	*P. perfoliatus* var. *bupleuroides*
	P. amplifolius
	P. pusillus var. *tenuissimus*
	P. gramineus var. *gramineus*
	P. alpinus var. *tenuifolius*
	P. natans
Group IV—alkalinity 48.9–73.2 mg HCO_3^- liter^{-1}	*P. richardsonii*
	P. praelongus
	P. obtusifolius
	P. zosteriformis
	P. alpinus var. *subellipticus*
	P. epihydrus var. *epihydrus*
Group V—alkalinity 73.3–109.8 mg HCO_3^- liter^{-1}	*P. pusillus* var. *pusillus*
	P. foliosus
	P. filiformis var. *borealis*
	P. illinoensis
	P. strictifolius
	P. crispus
	P. friesii
	P. nodosus
Group VI—alkalinity greater than 109.8 mg HCO_3^- liter^{-1}	*P. pectinatus*

passing many groups. The statistical means indicate the possibility of this classification which is similar to that of Spence (1967), except that Spence had three rather than six groups.

Group I (alkalinity 0.0–18.3 mg HCO_3^- liter $^{-1}$)

Group I in New England includes *Potamogeton* of "soft" waters, but under extreme circumstances ranging up to 48.8 mg. per liter with a mean less than 10.0 mg. per liter. All of the plants in this group are found mainly along the coastal plain.

Potamogeton confervoides is a plant of peaty ponds and soft water regions along the New England coastal plain. High altitude ponds of low alkalinity also contain this species. This is the only pondweed to be found in *Sphagnum* bog ponds in this study. The highest alkalinity encountered was 8.5 mg. per liter. *Potamogeton bicupulatus* (*P. capillaceus* Poiret) was abundant in the sandy-bottomed ponds of eastern New England, where only one location occurred with an alkalinity above 18.3 mg. per liter, the calculated upper limit for group I. *Potamogeton oakesianus* and *P. pulcher* were found in similar waters. The former was located at two areas where the alkalinity was above 18.3 mg. per liter, the highest being 23.8 mg. per liter. *Potamogeton pulcher* is the species which is most often found above the "soft" water limits of 18.3 mg. per liter, the highest being 46.4 mg. per liter. *Potamogeton pusillus* var. *gemmiparus* belongs in this group and tends to support the opinions of some botanists that this is an ecological variety. The narrow foliage of *P. pusillus* var. *gemmiparus* may be a growth form due to the low alkalinity, high acidity, or low nutrient content of the water. Steenis (1932) and Moyle (1945) in their studies did not include any of the above mentioned species from group I except *P. bicupulatus* (*P. capillaceus*). Steenis reported *P. bicupulatus* as occurring in very soft water.

Moyle (1945) and Hutchinson (1975) indicate that the pH may have an important role in plant distribution. Hutchinson (1975) notes that some species of *Potamogeton* do not occur perennially in waters with a pH below 6.0 whatever the calcium content. Hydrogen ion concentration data collected in New England indicates that 12 species of *Potamogeton* occur in some waters with a pH below 6.0. Most of these species are from group I or the ubiquitous group III (Hellquist, 1975)

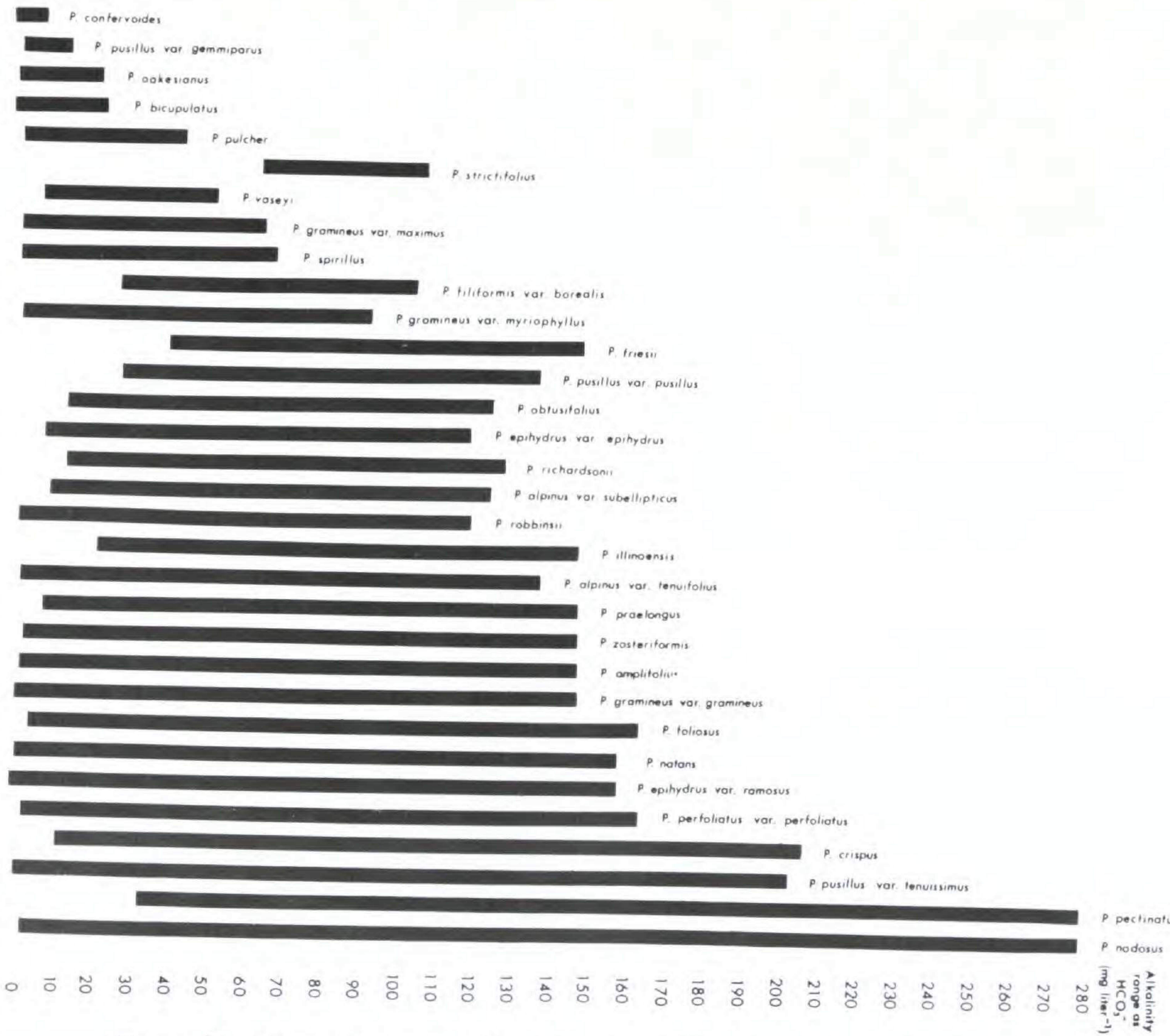

Figure 3. Alkalinity range of *Potamogeton* taxa from New England waters.

Group II (alkalinity 18.4–30.5 mg HCO_3^- liter^{-1})

Plants found in groups II–IV are considered to be of moderately alkaline waters. Moyle (1945) in Minnesota found *Potamogeton spirillus* to be the pondweed of the softest water and included it in the soft-water sub-group I of his classification. He included it with the soft-water plants *Eriocaulon septangulare* With. and *Lobelia dortmanna* L. Generally in New England, *P. spirillus* and *P. epihydrus* var. *ramosus* are considered plants of low alkalinity, but they may be found in harder waters, e.g. 60.4 and 69.9 mg. per liter for *P. spirillus* and many above 30.5 mg. per liter for *P. epihydrus* var. *ramosus*. Two of the three varieties of *P. gramineus* are in this group with *P. gramineus* var. *gramineus* in the next group. This may indicate an ecological difference, but the range of means for all three varieties has a width of only 20.1 mg. per liter. Moyle (1945) reported *P. gramineus* var. *graminifolius* f. *myriophyllus* (*P. gramineus* var. *myriophyllus*) from waters above 48.8 mg. per liter. This is considerably higher than found in New England except for one location (95.2 mg/l).

Potamogeton vaseyi and *P. robbinsii* are plants of wide geographical distribution in New England. *Potamogeton vaseyi* is confined to waters of a lower alkalinity range (8.5–54.9 mg/l) than *P. robbinsii* (3.7–122.0 mg/l).

Group III (alkalinity 30.6–48.8 mg HCO_3^- liter^{-1})

Four of the most commonly encountered taxa in New England occur in this group. These are *Potamogeton natans*, *P. gramineus* var. *gramineus*, *P. pusillus* var. *tenuissimus*, and *P. amplifolius*. These plants Moyle (1945) notes are common at all alkalinities in Minnesota. Ogden (1943) notes *P. amplifolius* as a plant of both alkaline and acid waters. Spence (1967) refers to *P. gramineus* as a ubiquitous plant. These statements hold true for these two plants in New England. The other two common pondweeds found throughout New England are in group II. These are *P. epihydrus* var. *ramosus* and *P. robbinsii*.

Potamogeton perfoliatus var. *bupleuroides* and *P. alpinus* var. *tenuifolius* are also included in this group. *Potamogeton perfoliatus* is more common along the coastal plain where it is found in waters with an alkalinity as low as 6.1 mg. per liter or in brackish ponds and streams. In western New England it occurs in harder waters up to 167.8 mg. per liter, often with the closely related *P. richardsonii*. *Potamogeton alpinus* has two poorly defined varieties in New England. *Potamogeton alpinus* var. *tenuifolius*, the more common variety, is found in waters with a lower alkalinity than is *P. alpinus* var. *subellipticus* of group IV. Both varieties are found in the northern portions of Maine, New Hampshire and Vermont.

Group IV (alkalinity 48.9–73.2 mg HCO_3^- $liter^{-1}$)

This group includes many of the hard-water plants of Moyle (1945), e.g. *Potamogeton richardsonii, P. praelongus*, and *P. zosteriformis*. In New England, plants of this group may occasionally occur in waters of lower alkalinity.

Potamogeton obtusifolius is common in northern Maine and northeastern Vermont where it occurs with *P. alpinus* in waters of moderate alkalinity usually below 67.1 mg. per liter. *Potamogeton epihydrus* var. *epihydrus* is also a plant of northern and western New England. This broad-leaved variety has an extremely limited distribution when compared with *Potamogeton epihydrus* var. *ramosus*.

Group V (alkalinity 73.3–109.8 mg HCO_3^- $liter^{-1}$)

Potamogeton of group V were found almost exclusively in alkaline waters of western New England and northern Maine, in the drainages of the Housatonic, St. Lawrence, Hudson, St. John rivers, and from regions of the Connecticut River drainage (Fig. 3). Moyle (1945) and McCombe and Wile (1971) found *P. crispus* in waters of high nutrients and high alkalinity. In Middlesex County, Massachusetts, *P. crispus* was found in waters with high nutrient levels but with an alkalinity of 24.4 mg. per liter or less. This plant evidently needs high alkalinity and/or high nutrient levels to survive.

Potamogeton nodosus is generally found in flowing water (Ogden, 1943). Moore and Clarkson (1967) found *P. nodosus* common in acid streams but not reproducing sexually. Clapham *et al.* (1962) indicate that in England it is found in deeper water along gravelly shores, or in slow-flowing alkaline waters. Moyle (1945) found it in waters of an alkalinity of 50.3–380.8 mg. per liter. In New England *P. nodosus* is common and often fertile in the Lake Champlain valley, especially in pasture streams and rivers of slow current. In eastern New England it is usually found in rivers of swift current with alkalinities below 18.3 mg. per liter. Here the plants are usually sterile. This pondweed appears to favor swift current if a higher alkalinity is not available, possibly because flowing waters are constantly delivering nutrients to the plants.

The remaining taxa in group V were mostly from waters of western New England. Three of these, *Potamogeton filiformis* var. *borealis, P. foliosus,* and *P. friesii* were also from northern Maine. *Potamogeton pusillus* var. *pusillus,* the third variety of this species, is found in this group. Wiegand and Eames (1925) indicate that *P. pusillus* var. *pusillus* is a plant chiefly of brackish or limey waters. It appears that in New England *P. pusillus* var. *gemmiparus* is of acid water, var. *tenuissimus* mainly of acid but also alkaline and brackish waters. Spence (1967) indicated that *P. filiformis* and *P. lucens* of Europe, the latter closely related to *P. illinoensis* of North America, were from calcareous lochs with alkalinities ranging from 42.7–191.6 mg. per liter. This is within the range of *P. illinoensis* in New England. *Potamogeton strictifolius* is rare in New England. During the present study it was found in quiet waters of only five ponds in Vermont. In two of the ponds it appears to have hybridized with *P. zosteriformis* to form the uncommon *P.* × *longiligulatus* (Hellquist, 1977).

Group VI (alkalinity greater than 109.8 mg HCO_3^- liter^{-1})

Potamogeton pectinatus was statistically isolated to group VI at higher alkalinities. This species occurs in alkaline and brackish water of New England. The two areas where it was found below an alkalinity of 48.8 mg. per liter were brackish ponds along the coast. Many authors (e.g. Metcalf, 1931; Moyle, 1945; Spence, 1967) have indicated that this plant is found in waters of extremely high alkalinity. In North Dakota, Metcalf (1931) found *P. pectinatus* mainly in brackish waters and did not consider it to be a fresh-water indicator. *Potamogeton pectinatus* in Minnesota occurs in waters with alkalinities ranging fromn 38.8 to 458.9 mg. per liter, and is considered a plant of hard and alkali water (Moyle, 1945).

Field studies conducted since this study indicate that *Potamogeton hillii* also belongs to this group. Ten locations as discussed by Hellquist (1977) and one additional site from 1978 field work indicate an alkalinity range of 105.8–316.7 mg. per liter with a mean of 174.5 mg. per liter and a median of 142.7 mg. per liter. Data from the one location in Maine and others in New York and Michigan indicate that *P. vaginatus* also belongs in group VI (Hellquist, 1977).

SUMMARY

The ranges of the alkalinities for New England taxa were found to compare favorably with those of Moyle (1945) from Minnesota. Certain New England taxa tolerated alkalinity ranges as low as, or lower than, their Minnesota counterparts, especially *Potamogeton robbinsii, P. zosteriformis, P. friesii, P. obtusifolius,* and *P. natans. Potamogeton nodosus* and *P. crispus* occurred at much lower alkalinities than previously reported. Taxa not reported from Minnesota or in sufficient numbers to be reported by Moyle were studied in New England. Plants of the acid water group I may not occur in Minnesota since its waters are not of a low enough alkalinity or pH. A few of these coastal plain species have been reported from Wisconsin and Michigan where favorable conditions exist.

A point that should be remembered is that the results from this study are statistically determined and in some cases offer excellent information to help further the knowledge of *Potamogeton* distribution. Plants in the field may often be found in habitats which seem completely alien to them but seem to do quite well, hence many exceptions exist.

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LITERATURE CITED

CLAPHAM, A. R., I. G. TUTIN, & E. F. WARBURG. 1962. Flora of the British Isles. 2 ed. Cambridge Univ. Press. Cambridge. 1269 pp.

FASSETT, N. C. 1957. A manual of aquatic plants. Univ. Wisconsin Press. Madison. 405 pp.

FERNALD, M. L. 1932. The linear-leaved North American species of *Potamogeton* section Axillaries. Mem. Am. Acad. Arts. Sci. **17:** 1–183.

———. 1950. Gray's manual of botany. 8 ed. American Book Co., New York. 1632 pp.

GLEASON, H. A. 1952. The new Britton and Brown illustrated flora of the northeastern United States and adjacent Canada. V. 1. Hafner Publishing Co., Inc. New York. 482 pp.

HAGSTRÖM, J. O 1916. Critical researches on the Potamogetons. Kong. Avenska Vetenskapsakad. Handl. **55:** 1–281.

HAYNES, R. R. 1974. A revision of the North American *Potamogeton* subsection Pusillii (Potamogetonaceae). Rhodora. **76:** 564–649.

HELLQUIST, C. B. 1975. Correlation of selected dissolved substances and the distribution of *Potamogeton* in New England. Ph. D. thesis. Univ. New Hampshire. 269 pp.

______. 1977. Observations on some uncommon vascular aquatic plants in New England. Rhodora **79:** 445–452.

HUTCHINSON, G. E. 1975. A treatise on limnology V. 3. Limnological botany. Wiley Press, New York. 660 pp.

MCCOMBE, A. M., & I. WILE. 1971. Ecology of aquatic vascular plants in southern Ontario impoundments. Weed Sci. **19:** 225–228.

METCALF, F. P. 1931. Wild-duck food on North Dakota lakes. U. S. Dep. Agric. Tech. Bull. no. **221.**

MOORE, J. A., & R. B. CLARKSON. 1967. Physical and chemical factors affecting vascular aquatic plants in some acid stream drainage areas of the Monongahela River. Proc. W. Va. Acad. Sci. **39:** 83–89.

MOYLE, J. B. 1945. Some chemical factors influencing the distribution of aquatic plants in Minnesota. Am. Midl. Nat. **34:** 402–420.

OGDEN, E. C. 1943. The broad-leaved species of *Potamogeton* of North America north of Mexico. Rhodora. **45:** 57–105, 119–163, 171–214.

REZNICEK, A. A. & R. S. W. BOBBETTE. 1976. The taxonomy of *Potamogeton* subsection Hybridii in North America. Rhodora. **78:** 650–673.

SPENCE, D. H. N. 1967. Factors controlling the distribution of freshwater macrophytes with particular reference to the lochs of Scotland. J. Ecol. **55:** 147–170.

STEENIS, J. H. 1932. Lakes of Sawyer County. Bull. Wis. Dep. Agric. and Markets. no. **138.**

THEROUX, F. R., E. F. ELDRIDGE, & W. L. MALLMAN. 1943. Laboratory manual for chemical and bacterial analysis of water and sewage. McGraw-Hill Book Co., Inc. New York. 274 pp.

WIEGAND, K. M., & A. J. EAMES. 1925. The flora of the Cayuga Lake basin, New York, vascular plants, Memoir **92.** Cornell Univ. Agric. Exp. Sta.

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